Botanical Sciences 102 (3): 686-697. 2024
DOI: 10.17129/botsci.3382

Received: July 31, 2023, Accepted: March 3, 2024
On line first: April 17, 2024

Ecology / Ecología

Crown cover of a dominant pioneer legume affects tree species regeneration in a secondary tropical dry forest

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Abstract
Background: Individual pioneer tree species often dominate early tropical dry forest succession and thereby affect possible successional pathways. *Mimosa acantholoba* var. *eurycarpa* is a highly dominant species in the tropical dry forest in Mexico.
Hypothesis: *Mimosa acantholoba* var. *eurycarpa* exerts an inhibitory effect on the germination, establishment, survival, and early growth of light-demanding pioneers, while facilitating these processes for shade-tolerant old-growth forests species.
Studied species: *Lonchocarpus torresiorum*, *Lysiloma divaricatum*, *Mimosa acantholoba* var. *eurycarpa* and *Vachellia farnesiana*.
Study site and dates: Nizanda, Oaxaca, Mexico, 2020-2021.
Methods: In 12 early successional plots, we applied three levels of crown cover removal (100, 50, and 0 %) of established trees of the dominant pioneer legume (*M. acantholoba* var. *eurycarpa*). We sowed seeds of the four study species in each experimental plot and recorded their germination, establishment, survival, and early growth over a 2-mo period.
Results: The removal of crown cover of established *M. acantholoba* var. *eurycarpa* trees did not significantly affect germination. *Lysiloma divaricatum* had the highest germination probability, the fastest germination, and the highest establishment probability regardless of treatment. *Lonchocarpus torresiorum* had the highest establishment probability in plots where the crown cover of established *M. acantholoba* var. *eurycarpa* trees was removed. The survival probability of both shade-tolerant species was highest in the 100 % removal treatment.
Conclusions: Despite successful germination of shade-tolerant species, their survival is inhibited under the dense canopy of the dominant legume. Therefore, interventions to reduce the crown cover area of this dominant legume may stimulate forest recovery.
Keywords: Crown cover removal, Dominant pioneer species, Forest recovery, Forest regeneration, Germination success, Seedling survival.

Resumen
Antecedentes: Las especies arbóreas pioneras que comúnmente dominan la sucesión secundaria temprana del bosque tropical caducifolio pueden afectar las posibles rutas sucesionales. *Mimosa acantholoba* var. *eurycarpa* es una especie muy dominante en el bosque tropical caducifolio de México.
Hipótesis: *Mimosa acantholoba* var. *eurycarpa* ejerce un efecto inhibitorio sobre la germinación, establecimiento, supervivencia y crecimiento inicial de especies pioneras intolerantes a la sombra, pero facilita estos procesos para especies de bosque maduro tolerantes a la sombra.
Especies de estudio: *Lonchocarpus torresiorum*, *Lysiloma divaricatum*, *Mimosa acantholoba* var. *eurycarpa* y *Vachellia farnesiana*.
Sitio y años de estudio: Nizanda, Oaxaca, México, 2020-2021.
Métodos: En 12 parcelas de sucesión secundaria temprana, aplicamos tres niveles de remoción de copa de *M. acantholoba*. Las cuatro especies de estudio se sembraron y registramos su germinación, establecimiento, supervivencia y crecimiento inicial durante dos meses.
Resultados: El tratamiento de remoción de la copa no afectó significativamente la germinación. *Lysiloma divaricatum* tuvo la mayor probabilidad de germinación, la germinación más rápida y la mayor probabilidad de establecimiento, independientemente del tratamiento. *Lonchocarpus torresiorum* tuvo la mayor probabilidad de establecimiento en las parcelas sin cobertura de copa de *M. acantholoba*. La probabilidad de supervivencia de ambas especies fue más alta donde *M. acantholoba* fue removida por completo.
Conclusiones: La germinación de las especies tolerantes a la sombra fue exitosa pero su supervivencia se inhibió por el denso dosel de *M. acantholoba*. La reducción de las copas de *M. acantholoba* puede estimular la recuperación de áreas forestales.
Palabras clave: Especies pioneras dominantes, Éxito germinativo, Recuperación forestal, Regeneración forestal, Remoción de copa, Supervivencia de plántulas.

Secondary forest succession is the process by which woody vegetation regrows after complete forest clearance for pasture, agriculture, other human activities, or natural disturbances. This process often results in a functional forest ecosystem but does not necessarily lead to the original pre-disturbance species composition (Guariguata & Ostertag 2001, Rozendaal *et al.* 2019). In the tropics, secondary forest succession involves several forces acting at multiple spatio-temporal scales, and certain conditions need to occur to allow the succession to proceed (Arroyo-Rodríguez *et al.* 2017, Chazdon 2017).

In the tropical dry forests (TDF) of the Neotropics, pioneer species belong mainly to the Fabaceae family, with as much as 37 % of the basal area in the first 10 years of succession belonging to this family, compared to an average of 18 % in wet forests (Gei *et al.* 2018). The microclimatic conditions at the initial and early stages of succession in TDFs are more stressful for plant life than in wet forests (Ceccon *et al*. 2006, Lebrija-Trejos *et al.* 2008). In these successional stages, pioneer species facilitate the establishment of less tolerant tree species, as the shaded environment beneath their canopy may dampen extreme temperature and improve soil water retention (Badano *et al.* 2009, Chapin *et al.* 2011, Williams-Linera *et al.* 2011).

In secondary TDFs across Mexico, 80 % of the aboveground biomass is recovered during the first 25 years of succession with only few species (≤ 18 species) being involved, including several species in the genus *Mimosa* (Rozendaal *et al.* 2017). In Nizanda, Mexico, only two pioneer legumes, namely *Mimosa acantholoba* (Humb. & Bonpl. ex Willd.) Poir. var. *eurycarpa* (B.L.Rob.) Barneby and *M. tenuiflora*, account for that percentage (Lebrija-Trejos *et al.* 2008). These dominant species may potentially have a strong impact on the successional pathways in the areas where they occur. For example, some studies have reported that early successional *Mimosa* species provide benefits to degraded areas mainly by increasing soil nutrient availability and improving environmental conditions such as temperature and moisture (Camargo-Ricalde *et al.* 2002, 2010, dos Reis Jr *et al.* 2010, Bhaskar *et al.* 2016), suggesting a potential role as nurse plant for other species (Valiente-Banuet & Ezcurra 1991, Badano *et al.* 2009). However, most studies have focused on isolated individuals acting as nurse plants compared with areas without vegetation. The high dominance and high-density of single pioneer species result in closed canopies that may potentially interfere with the establishment and subsequent development of old-growth forest species in the understorey.

Resources and propagule availability stimulate natural forest recovery. Seed availability is a major limiting factor when seed banks of pastures and agricultural fields have low density of tree species, when seed dispersal is lacking, or when seed predation is high, limiting the available pool of species (Wijdeven & Kuzee 2000, Bonilla-Moheno & Holl 2010, Chazdon 2017, Dent & Estrada-Villegas 2021). In the seed bank of recently abandoned lands in Nizanda, woody pioneer and old-growth forest species are extremely scarce (Meave *et al.* 2012). Therefore, a better understanding of the processes determining the natural regeneration of trees during succession is key to enhance forest recovery (Sampaio *et al.* 2007). Natural regeneration can be increased through enrichment planting, or can be assisted through fire protection, weed control, liberation from competitors and herbivores. All these methods have lower costs than large-scale tree planting approaches (Chazdon 2017).

Most seed germination and seedling early development studies for tropical dry forest species have been conducted in laboratories, greenhouses or nurseries, which may have limited correspondence with field conditions (Hoffman *et al.* 1989, Cervantes *et al.* 1998, McLaren & McDonald 2003, Vieira & Scariot 2006, Soriano *et al.* 2011, Cervantes *et al.* 2014). Although field experiments in TDF are slowly increasing, they are still scanty (Orozco-Almanza *et al.* 2003, Camargo-Ricalde *et al.* 2004, González-Rivas *et al.* 2009, Alvarez-Aquino *et al.* 2014, de Souza Gomes Guarino & Scariot 2014).

Given that early pioneers, such as various *Mimosa* and other legume species, may strongly impact future vegetation development and successional pathways, we need to discern whether these species act mainly as facilitators (nurse plants), a phenomenon that has been observed in other forest ecosystems (Avendaño-Yáñez *et al*. 2016), or whether they mostly arrest/inhibit germination, establishment, survival, and early growth of other species in early successional stands. Here, we report the results of a crown cover removal experiment of the dominant *M. acantholoba* var. *eurycarpa* (hereafter referred to as *M. acantholoba*), considering that crown cover directly affects the understorey environment. Our goal was to determine the effect of the amount of crown cover of the dominant legume *M. acantholoba* on the germination, establishment, survival, and early growth of pioneer and old-growth forest species. Given the poorly-lit conditions created by the closed canopy of this dominant species in the understorey of early successional TDF, we hypothesized that this species exerts an inhibitory effect on the germination, establishment, survival, and early growth of light-demanding pioneers, while facilitating these processes for shade-tolerant old-growth forests species. Therefore, we predicted an increasing performance of pioneer species with a decreasing influence (*e.g.* canopy cover) of the dominant pioneer but the opposite trend for the old-growth species.

Methods

Study site. This study was conducted in the tropical dry forest region of Nizanda, Oaxaca state, southern Mexico (Figure 1). Mean (± SD) annual temperature is 27.6 ± 0.6 °C, and average annual rainfall is 902.6 ± 351.2 mm, with a highly seasonal precipitation falling mainly from mid-June to mid-October (clicom-mex.cicese.mx). Although mechanized agriculture is being promoted, most local people still practice traditional slash-and-burn agriculture; around Nizanda, fields are typically cultivated for one or two years before abandonment, which results in the presence of a mosaic of differently-aged fallows spread across the area (Gallardo-Cruz *et al.* 2012).

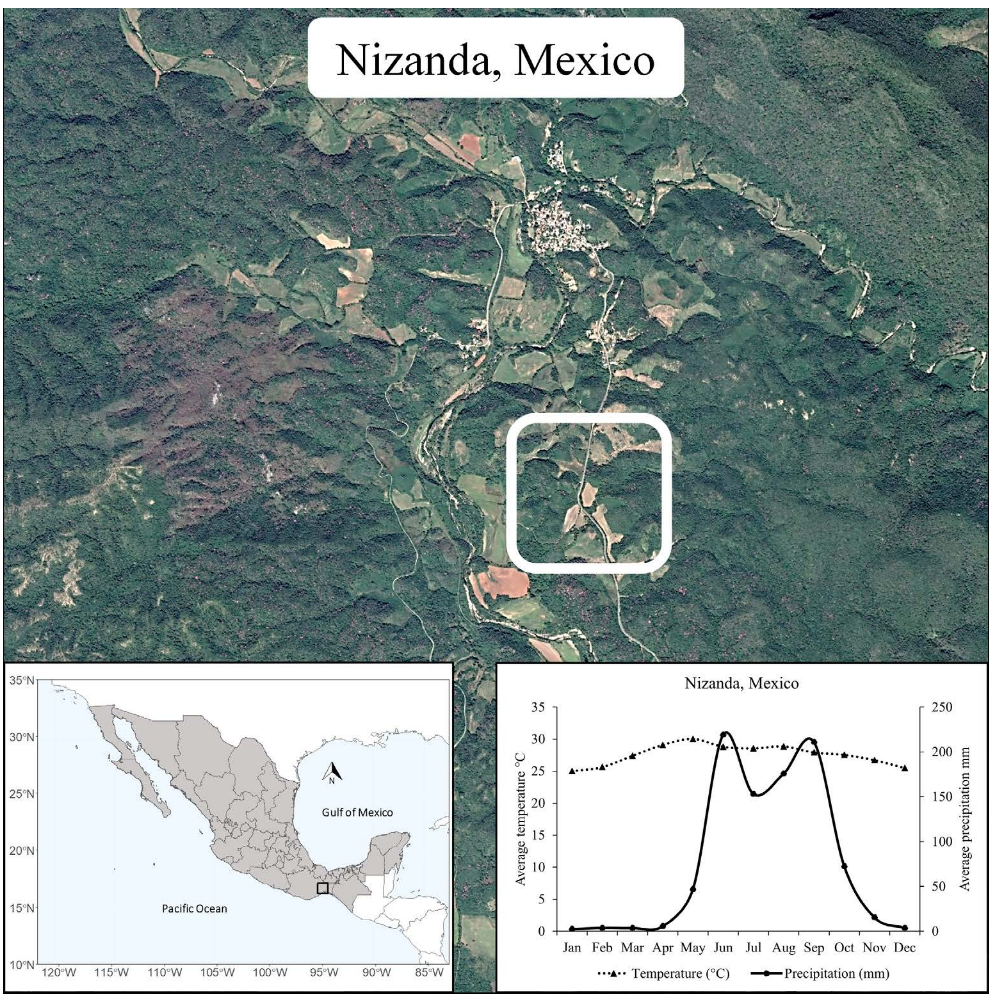

Figure 1. Location of the study site in Nizanda, Oaxaca, Mexico. The white square shows the area where the 12 experimental plots were established for this study. The climatic diagram shows the annual precipitation and temperature patterns in the region.

Experimental design and data collection. For the crown cover removal experiment, we selected four young secondary forest stands dominated by *M. acantholoba*. All selected areas had been abandoned 10 years prior to the study after being used for 1-2 years as fields for maize and squash production. At each site, we established one 20 × 60 m block, which was in turn divided in three 20 × 20 m (400 m^2) plots, which are the experimental units for the crown cover removal. These plots were randomly assigned to one of three treatments: 0 % (no removal, hereafter control), 50 and 100 % removal of *M. acantholoba* crown area. This means that the experimental crown cover removal was done at the community rather than at the individual tree level. We measured the crown area of all *M. acantholoba* individuals in each plot to determine the amount of crown area to be removed, and then cut down randomly selected individuals ≥ 1 cm DBH until achieving the necessary removal level. The initial densities of *M. acantholoba* per plot differed, but treatments were distributed across the different densities. The crown area removed for plots with 50 % removal ranged between 150.5 and 646.3 m^2 (28 to 95 trees), and for the 100 % removal was between 343.1 and 606.7 m^2 (86 to 119 trees). The experimental set up was maintained by subsequently removing individuals that resprouted.

To evaluate the effect of crown cover removal of *M. acantholoba* on germination, establishment, survival, and early growth of focal tree species, we set up a seed germination experiment, using four Fabaceae species present in the region; two of them were the pioneer species *M. acantholoba* and *Vachellia farnesiana* (L.) Wight & Arn. (light-demanding), whereas the other two were the old-growth forest species *Lonchocarpus torresiorum* M.Sousa and *Lysiloma divaricatum* (Jacq.) J.F.Macbr (shade tolerant). The seeds of the four species are orthodox, and the seeds of these species in the region were measured in a previous study (Cervantes Jiménez 2015), the sizes in the same order mentioned are 3.8 × 3.3 × 1.6 mm, 6.5 × 3.9 × 2.4 mm, 12.4 × 8.2 × 3.5 mm, and 6.6 × 5.0 × 2.1 mm. The weight of the seeds of *V. farnesiana* is 75.99 g per 1,000 seeds and for *Lysiloma divaricatum* 31.48 g per 1,000 seeds (ser-sid.org). Seeds that are larger and heavier possess larger reserves, thereby contributing to a higher germination percentage, enhanced survival, and increased growth (Khurana & Singh 2001). *Mimosa* species have a tough seed coat (Orozco-Almanza *et al*. 2003). The selection of these species was determined by their high frequency in the area and the possibility to obtain enough seeds prior to insect infestation. Seeds were collected in the dry season from 5-8 healthy-looking trees per species. Seeds were removed from the fruits; only those without visible damage were stored in glass flasks and checked for viability through flotation in water just before sowing them. No additional mechanical or chemical seed scarification was applied to maintain the natural conditions of the experiment as much as possible, regardless that seed dormancy could play a role in the germination success (Cortés-Flores *et al*. 2020).

For the seed germination experiment, 50 seeds per species were sown on the ground at systematic locations of each of the 12 plots during the rainy season. Seeds were sown at 1 cm depth to avoid desiccation and with a distance of 10 cm among them, within a 0.5 × 1 m area. In total, 200 seeds per species per removal treatment were sown. A seed was recorded as germinated upon the emergence of the cotyledons; later, a plant was tallied as established when the first true leaves developed. Germination records started on the third day after sowing; initially, observations were made daily for six weeks and later once per week for two more weeks (*i.e.*, a total of eight weeks of monitoring). Twelve weeks after the start of the experiment, the height and diameter at ground level of alive plants were measured. After seeds were first sown, no further management was performed in the plots around seedlings to guarantee that only the effect of the removal treatment was evaluated.

Data analysis. To test the hypothesis that in early successional forest *M. acantholoba* inhibits the germination, establishment, survival, and early growth of pioneers, while facilitating old-growth forests species, we calculated three germination indices (germination percentage, mean germination time, and germination speed) using the GerminaR package (Lozano-Isla *et al.* 2019). Two-way ANOVA was used to determine whether the germination indices differed among species and treatments using the stats package (R Core Team 2020). A time-to-event analysis was performed to compare the germination probability per species in the different removal treatments using the Kaplan-Meier estimate; probability curves were pairwise compared with the log-rank test (Kleinbaum & Klein 2012). In this analysis, right-censored seeds (*i.e.*, seeds that did not germinate during the monitoring) were included. The same analysis was used to compare the establishment probability; right-censored germinated seeds (*i.e.*, germinated seeds that did not show the first true leaves during the monitoring) were included. Time to establishment was recorded from the germination date (*i.e.*, since the emergence of the cotyledons). The Kaplan-Meier estimate was used again to perform a survival analysis to compare the survival probability of germinated plants; the survival curves were compared with the log-rank test. Time to death was recorded from the germination date. In this analysis, right-censored plants (*i.e.*, plants that did not die during the monitoring) were included. These analyses were carried out using the survival (Therneau 2020) and survminer (Kassambara *et al.* 2021) packages of R. Finally, to analyse the effect of the removal treatment on the height and diameter at ground level of the alive plants at the end of the experiment, we use two-way ANOVA, with species and treatment as factors. This analysis was done using the stats package (R Core Team 2020).

Results

Seed germination. Seed germination percentage differed significantly among species (ANOVA, $F_{3,36} = 209.15$, $P < 2 \times 10^{-16}$), but not among treatments ($F_{2,36} = 0.4239$, $P = 0.6577$), and the species × treatment interaction was not significant ($F_{6,36} = 0.2276$, $P = 0.9651$). The old-growth forest species *Lonchocarpus torresiorum* (12 - 19 %) and *Lysiloma divaricatum* (76.5 - 79.5 %) had higher seed germination percentages than the pioneers *Mimosa acantholoba* (2.5 - 3.5 %) and *Vachellia farnesiana* (0.5 - 1.0 %) in all treatments. Because of the low seed germination of the pioneer species (zero for some replicates and almost zero for others), we were only able to conduct further analyses for old-growth forest species.

Seed germination percentage (Figure 2A) did not differ among treatments ($F_{2,18} = 0.4511$, $P = 0.6440$), but differed between the two old-growth forest species ($F_{1,18} = 159.64$, $P < 2.2 \times 10^{-10}$), and the species × treatment interaction was not significant ($F_{2,18} = 0.1039$, $P = 0.9018$). Mean germination time did not differ among treatments ($F_{2,17} = 0.9161$, $P = 0.4189$), but differed between the two species ($F_{1,17} = 19.55$, $P = 0.0004$), and the species × treatment interaction was not significant ($F_{2,17} = 1.1232$, $P = 0.3482$). *Lysiloma divaricatum* seeds required fewer days to germinate than *Lonchocarpus torresiorum* (Figure 2B). Similarly, germination speed (Figure 2C) did not differ among treatments ($F_{2,17} = 2.4123$, $P = 0.1196$), but differed significantly between the two species ($F_{1,17} = 448.79$, $P = 1.2 \times 10^{-13}$) and the species × treatment interaction was also not significant ($F_{2,17} = 2.9784$, $P = 0.0778$).

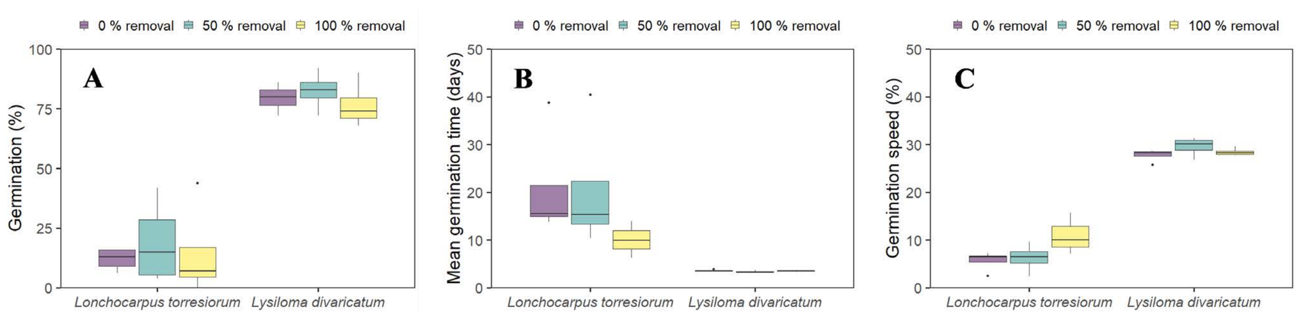

Figure 2. Mean values (± SE) of germination indices for the shade-tolerant species *Lonchocarpus torresiorum* and *Lysiloma divaricatum* in three *Mimosa acantholoba* var. *eurycarpa* crown cover removal treatments (0 % [control], 50 %, and 100 % removal) in a tropical dry forest of southern Mexico. (A) Seed germination percentage. (B) Mean germination time. (C) Germination speed.

Lysiloma divaricatum had a higher germination probability than *Lonchocarpus torresiorum*. The germination probability of these species was not affected by treatment (for *Lonchocarpus torresiorum*: log-rank test, $\chi^2(2) = 4.3$, $P = 0.1$, for *Lysiloma divaricatum* was marginally significant: $\chi^2(2) = 5.5$, $P = 0.06$; Figure 3A, B).

Seedling establishment and survival. Seedling establishment probability of *Lonchocarpus torresiorum* differed among treatments (Figure 3C, log-rank test, $\chi^2(2) = 11.8$, $P = 0.003$), with the establishment probability increasing with crown cover removal. According to the results of the pairwise comparison, the 50 % removal and 100 % removal treatments were not significant different (log-rank test, $P = 0.5316$). For *Lysiloma divaricatum*, the treatment had no effect (Figure 3D, $\chi^2(2) = 0.2$, $P = 0.9$).

Survival probability of *Lonchocarpus torresiorum* differed significantly among treatments (Figure 3E, $\chi^2(2) = 10.8$, $P = 0.005$), with the survival probability increasing with crown cover removal. The results of the pairwise comparison did not show a significant difference between the 50 % removal and the control (log-rank, $P = 0.3499$). Similarly, *Lysiloma divaricatum* showed significant differences among all treatments (Figure 3F; long-rank test, $\chi^2(2) = 118$, $P < 2 \times 10^{-16}$), with the survival probability also increasing with crown cover removal. The pairwise comparison of the survival curves revealed that the three of them were significantly different from each other (log-rank test, control *vs*. 50 % removal, $P = 2 \times 10^{-13}$; control vs. 100 % removal, $P < 2 \times 10^{-16}$; 50 % removal vs. 100 % removal, $P = 0.0096$).

Plant size. Twelve weeks after the seeds were sown, plant height differed significantly between species (ANOVA, $F_{1,319} = 8.34$, $P = 0.0041$) but not among treatments ($F_{2,319} = 2.76$, $P = 0.0646$), with plants of *Lonchocarpus torresiorum* being taller than plants of *Lysiloma divaricatum*. The interaction term was not significant ($F_{2,319} = 1.86$, $P = 0.1574$). By contrast, diameter at ground level did differ significantly among treatments ($F_{2,319} = 31.65$, $P = 2.9 \times 10^{-13}$) and species ($F_{1,319} = 499.45$, $P < 2.2 \times 10^{-16}$), and the interaction between these terms was also significant ($F_{2,319} = 11.04$, $P = 2.3 \times 10^{-5}$). *Lonchocarpus torresiorum* had larger mean diameter at ground level than *Lysiloma divaricatum* but the diameter at ground level of the latter species (*Lysiloma divaricatum*) did increases with the crown cover removal. In general, *Lonchocarpus torresiorum* showed better growth than *Lysiloma divaricatum*.

Discussion

To accelerate forest recovery, knowledge of seed germination and seedling establishment in the complex environmental conditions of the field is required. In this study, we evaluated the impact of the dominant early successional dry forest pioneer species *Mimosa acantholoba* var. *eurycarpa* on the regeneration (*i.e.*, germination, establishment, survival, and early growth) of two pioneer (*M. acantholoba* and *Vachellia farnesiana*) and two old-growth forest species (*Lonchocarpus torresiorum* and *Lysiloma divaricatum*). For doing so, we carried out an experiment with three crown cover removal treatments of the dominant species. We deliberately did not apply any pre-germination treatment to allow germination to occur under natural conditions in the field. We found differences in germination indices for species but not for treatments. In particular, crown cover did not affect germination of the old-growth forest species but inhibited their survival. The survival probability and diameter at ground level was higher in plots where the crown cover of *M. acantholoba* was experimentally removed at various levels.

Germination. Germination percentage differed among species, with the pioneers *M. acantholoba* and *V. farnesiana* having much lower germination success than the old-growth forest species, especially when compared with the high germination percentage of *Lysiloma divaricatum*, which also needed fewer days to germinate. Differences in germination percentages appear to be unrelated to seed size; although we originally expected the larger reserves of bigger and heavier seeds to promote their germination (Khurana & Singh 2001), this was not the case. Seeds of the species with the most successful germination (*Lysiloma divaricatum*) have a similar size (6.6 × 5.0 × 2.1 mm) to seeds of *V. farnesiana* (6.5 × 3.9 × 2.4 mm). In turn, *Lonchocarpus torresiorum* has bigger seeds (12.4 × 8.2 × 3.5 mm) than all other study species (Cervantes Jiménez 2015), but its germination success was lower than that of *Lysiloma divaricatum*. In TDFs, seed germination is often limited by water (Vieira & Scariot 2006), but in this experiment we did not expect plants to experience strong water limitations as the experiment was carried out in the rainy season. Additionally, seeds of *V. farnesiana* have been reported to germinate under water stress (Khurana & Singh 2001).

The low germination percentage of the two pioneer species may be due to unsuccessful dormancy breakage under field conditions. Germination experiments of tropical dry forest species have shown that seeds that underwent scarification treatments have higher germination rates than those without scarification (Cervantes *et al.* 1996, Orozco-Almanza *et al.* 2003, Camargo-Ricalde *et al.* 2004, Pavón *et al.* 2011, Alvarez-Aquino *et al.* 2014). For scarified seeds of *Mimosa* species, germination was above 90 % in the field under the canopy of *Mimosa* species (Orozco-Almanza *et al.* 2003, Camargo-Ricalde *et al.* 2004), whereas for *Acacia cochliacantha, Caesalpinia cacalaco,* and *Ipomoea wolcottiana*, germination percentage for scarified seeds ranged between 47.2 and 97.2 % (Alvarez-Aquino *et al.* 2014), and for *V. farnesiana* around 90 % (Cervantes *et al.* 1996).

Germination percentage and germination probability of the old-growth forest species did not differ among the crown cover removal treatments (Figure 2A and 3A-B). These results contradict our prediction that shade-tolerant species would have higher germination in the *Mimosa* dominated plots, as well as results of other studies; for example, McLaren & McDonald (2003) showed that shaded nursery plots were associated with higher germination percentages than unshaded plots for the tropical dry forest species *Calyptranthes pallens*, *Eugenia* sp., *Hypelate trifoliata* (reported by the authors as *Hypelate trifolia*) and *Metopium brownei*. Similarly, in a study carried out in moist forest stands differing in age (plots < 5 yr, 8 - 15 yr, and > 50 yr), direct seeding of *Manilkara zapota* resulted in higher germination in the older forest than in the younger ones, while direct seeding of *Brosimun alicastrum and Enterolobium cyclocarpum* resulted in similar germination across ages (Bonilla-Moheno & Holl 2010). In our study, we did not find an effect of crown cover removal of *M. acantholoba* on germination, indicating that this species does not facilitate the germination of the studied shade-tolerant species, as we had expected.

Establishment, survival, and early plant growth. We expected higher seedling establishment (*i.e.*, from cotyledon emergence to production of first true leaves) in control plots where *M. acantholoba* crown cover was not removed. However, we found that the removal treatment was unrelated to the seedling establishment probability of *Lysiloma divaricatum* (this species has a high establishment probability under all conditions) and for *Lonchocarpus torresiorum* seedling establishment probability was higher in plots where *M. acantholoba* crown cover was removed (Figure 3C-D). *Lonchocarpus torresiorum* actually benefits from a lower crown cover than it is normally the case in *M. acantholoba* dominated secondary forests, as extreme shading conditions decrease the success of seedling establishment in TDF (Vieira & Scariot 2006).

The survival probability for the two old growth forest species (*Lonchocarpus torresiorum* and *Lysiloma divaricatum*) was higher in the 100 % removal treatment (Figure 3E-F), in contrast with our initial expectation. This result is in partial agreement with previous studies showing that seedling survival probability of tropical dry forest species is higher under mixed species plots than in single species dominated plots (Alvarez-Aquino & Williams-Linera 2012, Dimson & Gillespie 2020), as is the case of plots dominated by *M. acantholoba*.

We expected young plants to attain larger sizes (*i.e.*, larger heights and diameters at ground level) in plots where the removal treatments were applied. Such increased growth was observed for seedlings growing under the experimental removal of the exotic species *Chromolaena odorata* which forms a very dense canopy in degraded TDF in Ghana (Honu & Dang 2000). However, in our experiment plant height did not differ among treatments, despite the significant differences recorded between species. Interestingly, Bonilla-Moheno & Holl (2010) report similar results for *Brosimun alicastrum*, *Enterolobium cyclocarpum* and *Manilkara zapota* saplings growing in moist forest stands of different ages. Intriguingly, not all plant size indicators showed the same pattern, which underscores the need to use more than one size indicator when assessing growth of young plants under experimental conditions. For instance, diameter at ground level did differ between species and among treatments, but this was not the case of plant height.

Management implications. Although pioneer species used as isolated nurse trees in open spaces are beneficial for the regeneration of late successional species (Valiente-Banuet & Ezcurra 1991, Badano *et al.* 2009, Paterno *et al.* 2016), their effects when they grow in high densities have seldom been examined. When the dominance and high densities of *M. acantholoba* persist for decades, the successional process may be slowed down or temporarily arrested. Hence,

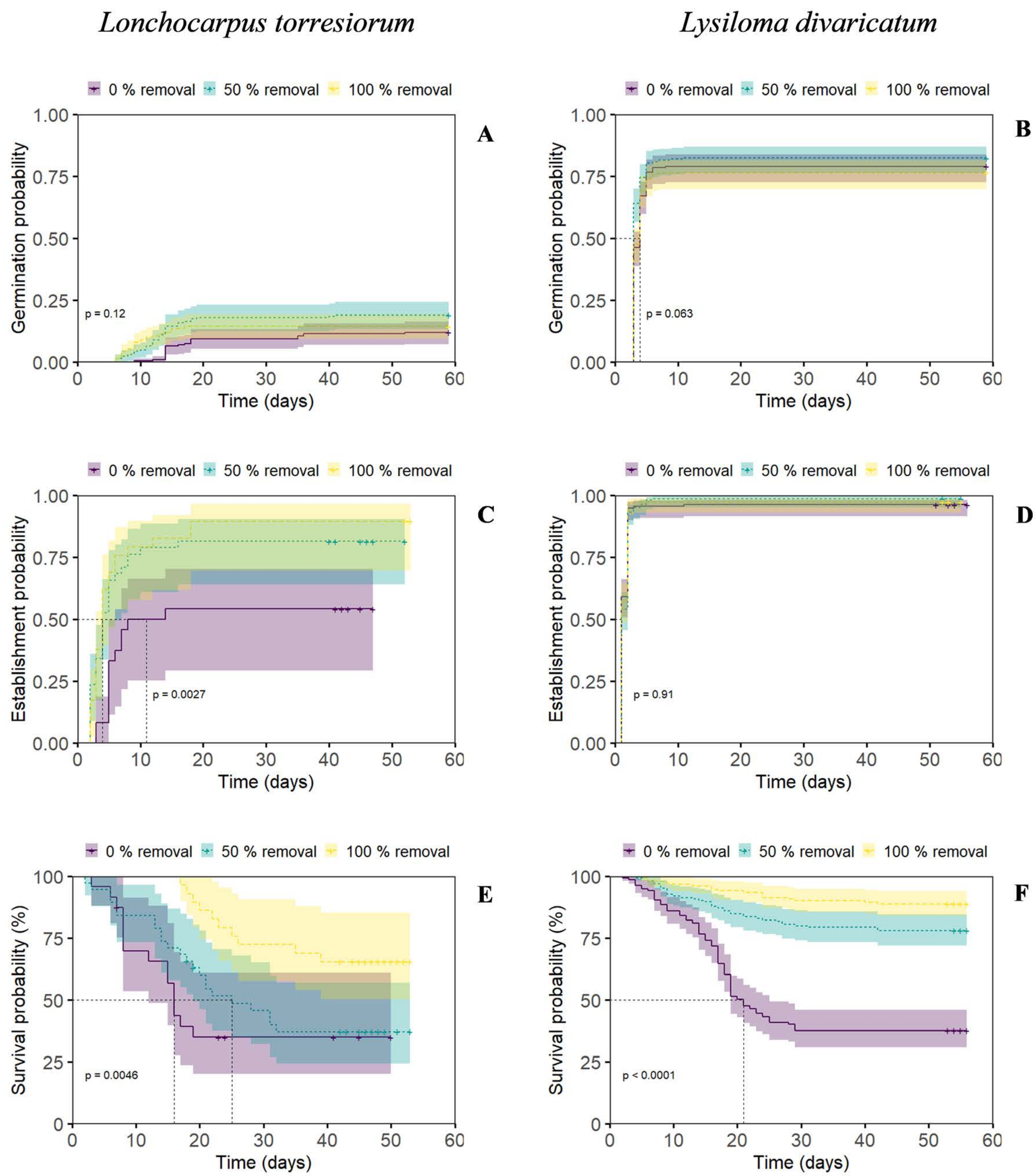

Figure 3. Germination probability curves (A-B), establishment probability curves (C-D) and seedling survival probability curves (E-F) for two old-growth tree species (*Lonchocarpus torresiorum* left and *Lysiloma divaricatum* right) per *Mimosa acantholoba* var. *eurycarpa* crown cover removal treatment (0 % [control], 50 %, and 100 % removal) in a tropical dry forest of southern Mexico. *p*-values are based on log-rank test. The shaded area indicates the 95 % confidence interval.

proper intervention when this dominant species attains the highest densities during succession (around 10 years after land abandonment), removal of a fraction of these individuals may substantially accelerate forest recovery (Honu & Dang 2000, Vieira & Scariot 2006), as suggested by the higher survival observed for the two old-growth forest species in this experiment.

Seed availability is a major limiting factor in TDF recovery, as seed density of tree species in agricultural and post-agricultural seed banks is extremely low and does not match the canopy composition of later successional and old-growth forest (Wijdeven & Kuzee 2000, Meave *et al.* 2012, Alvarez-Aquino *et al.* 2014). In Nizanda, the presence of old-growth forest species in successional stands has been recorded from early stages, but less frequently than in old-growth forest (Lebrija-Trejos *et al.* 2008). Without management, the early stage of succession will be mostly limited to the species initially present in the pastures and to those with sprouting ability. Considering that planting is expensive, seeding could be used as a supplementary technique to reduce the costs of restoration efforts (Sampaio *et al.* 2007).

For species that slowly colonize the TDF understorey, direct seeding is a potentially good strategy to enhance the presence of old-growth forest species in early secondary succession, where the canopy of pioneer species can provide a suitable environment for their establishment. For example, Fabaceae species can help reducing nitrogen and phosphorus limitations (Khurana & Singh 2001, Bonilla-Moheno & Holl 2010, Chazdon & Guariguata 2016). The incorporation of mature forest species into the successional process at very early stages and the recruitment of individuals through resprouting may facilitate the recovery of the TDF (Williams-Linera *et al.* 2011). Direct seeding can be more effective if applied for species with high germination and seedling survival rates. According to our results, direct seeding of old-growth forest species, as is the case of *Lysiloma divaricatum* and *Lonchocarpus torresiorum*, may efficiently increase their densities in early successional stands, where a canopy of pioneer species is well developed. As suggested by Bonilla-Moheno & Holl (2010), recently abandoned areas (< 5 years) appear to be less suitable, given the much lower germination percentages recorded in them.

Under a *M. acantholoba* dominated canopy, *Lysiloma divaricatum* seems a suitable species for direct seeding, as under this condition it has high germination percentage and short time for germination. In addition, this species neither appears to require a pre-germination treatment nor high technification or training, all of which is desirable in places where high investments for forest restoration are unfeasible (Chazdon & Guariguata 2016). Given that *Lysiloma divaricatum* is a typical mature forest species (Lebrija-Trejos *et al.* 2008), the sooner this species takes over in succession, the faster habitat availability will increase for other old-growth forest species.

Seed availability of woody species in recently abandoned fields is limited and dominant *M. acantholoba* var. *eurycarpa* remains in the system for decades. In young secondary TDF, this dominant species does not have an effect on germination but it does influence succession by reducing the survival of young seedlings. Our results suggest that the removal of at least 50 % of the crown cover of *M. acantholoba* in early succession stimulates the development of other species during the rainy season. From the two old growth forest species used for the germination experiment, *Lysiloma divaricatum*, a typical dominant species in the old-growth TDF, has the higher germination without any scarification treatment, which makes it suitable for direct seeding in young secondary TDF plots to secure its presence and density in early succession. Then, *Lysiloma divaricatum* will overcome *M. acantholoba* and may stimulate the development of other old-growth forest species, thereby accelerating forest recovery. Clearly, the regeneration of species with different successional affinities in early successional stands depends on the conditions created along experimental gradients of crown cover of dominant species, and thus we encourage using this approach to efficiently put the recovery of this threatened ecosystem on the fast track.

Acknowledgements

We thank all the fieldwork assistants who helped us to set up this experiment and collected the data in Nizanda, Mexico. We acknowledge the constructive feedback of two anonymous reviewers on an earlier version of this article.

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Associate editor: Joel Flores

Author contributions: USR: Conceptualization, Investigation, Visualization, Writing - original draft, Writing - review & editing, Project administration. MPC: Conceptualization, Supervision, Writing - review & editing. RDLM: Field work. JAM: Conceptualization, Funding acquisition, Supervision, Project administration, Writing - review & editing. FB: Conceptualization, Investigation, Funding acquisition, Supervision, Writing - review and editing.

Supporting Agencies (alphabetical order): Consejo Nacional de Ciencia y Tecnología (CONACYT), Graduate Scholarship (to USR). Dirección General de Asuntos de Personal Académico-UNAM, grant PAPIIT IN217620 (to JAM).

Conflict of interest: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.